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Soil Weathering Stage, Vegetation Succession, and Canopy Dieback[1]

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ABSTRACT: A conceptual model that provides a means of viewing changes in vegetation as responses to weathering of soil mantles over thousands of years has been developed from investigations of vegetation communities on a soil chronosequence on sand dunes extending back in time to at least the last interglacial. Progressive and retrogressive phases in natural plant succession are indicated by this sequence. A similar model is used to postulate that the various canopy dieback symptoms and agents observed in the New England tablelands of New South Wales, Australia, represent the mechanisms by which changes are occurring in retrogressive ecosystems that have been disturbed by human land use. We suggest that investigations of the etiology of diebacks need to be made in the context of temporal changes in soil fertility associated with the degree of soil weathering.

TREE DEATH IS ASSOCIATED with a wide range of causal agents and processes, which may act singly or in complex interactions. Some of the most important are (1) senescence; (2) competition among individuals for resources (physiological stress); (3) cyclic or single catastrophic physical environmental events; (4) pathogens (natural or introduced); (5) insect predation (leaf eaters, leaf suckers); and (6) anthropogenic disturbance (fire, machinery). In addition, investigations of the etiology of diebacks need to be made in the context of temporal changes in soil fertility associated with the degree of soil weathering. The degree of soil weathering may exercise a primary control through differential impacts on the vulnerability of trees to other forms of stress. The degree of soil weathering is reflected in the biological and nutrient characteristics of the soil, called "soil biological age" by Stark (1978), which we suggest may be relevant with respect to some phenomena.

An understanding of our interpretation of the concept of plant succession and, in particular, the difference between progressive succession and retrogressive succession is basic to our hypothesis. Noble and Slatyer (1980:135) suggested that "the established view of succession is that, following a disturbance, several assemblages of species progressively occupy a site, each giving way to its successor until a community finally develops which is able to reproduce itself indefinitely." This definition implies an orderly process that is reasonably directional and predictable, and culminates in a self-sustaining stable system. Such changes in vegetation may be termed "progressive succession" (Figure 1*a*). It has been deduced (Walker and Thompson 1981) that vegetation disturbed during the progressive phase of succession will return to a preexisting state only at the young and intermediate soil developmental stages, where nutrient inputs can still compensate for nutrient losses. As the soils become deeply weathered over a long period and their nutrient reserves are depleted, "retrogressive succession" occurs, in which biomass levels are sequentially reduced and species composition permanently altered in a less predictable fashion (Figure 1*b*).

A conceptual model that provides a means of viewing changes in vegetation as responses to weathering of soil mantles over thousands of years has been developed from investiga-

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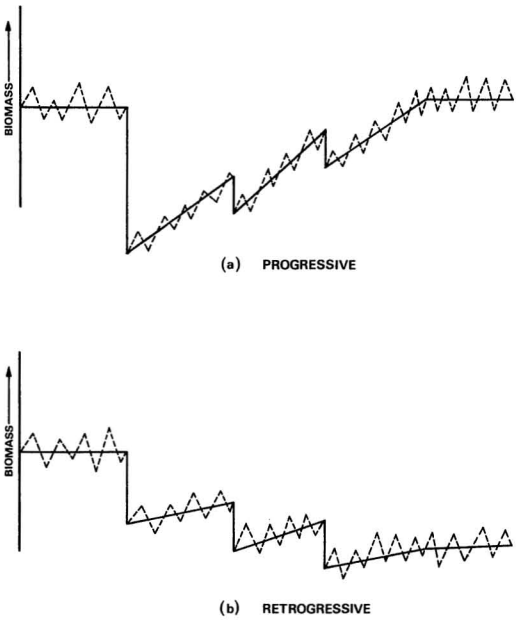

FIGURE 1. The effect of disturbance on progressive and retrogressive forest systems that are in a pseudo-steady state prior to disturbance. The progressive system has the potential to return to its previous state; the retrogressive system has an increased tendency to change to a lower biomass state.

tions of vegetation communities on a soil chronosequence on sand dunes extending back in time to at least the last interglacial (Walker et al. 1981). A similar model is used here to postulate vegetation changes in the tablelands of New South Wales, Australia. In the latter areas, vegetation changes are associated with particular land uses that may have accelerated canopy dieback as a result of changed soil conditions analogous to different stages of soil weathering (biological ages of the soils).

VEGETATION RESPONSES TO SOIL AGING

Most of Australia escaped the direct effects of the Pleistocene glaciations, which destroyed the Tertiary landscapes and weathering mantles over much of the northern hemisphere. As a consequence, landscapes and weathering mantles initiated during the Tertiary persisted in Australia and elsewhere in the tropics, and were later modified by erosion and weathering during the Quaternary (Beckmann 1983, D'Hoore 1956). Where the rates of weathering have continued to exceed geological erosion, the residual products of weathering have formed thick soil mantles that generally lack weatherable minerals and have very low contents of available plant nutrients. Examples are the extensive areas of lateritic soils in Australia, the large areas of giant podzols (quartzipsamments) on white sands (Bleackley and Khan 1963, Klinge 1965, Richards 1941), and many of the lateritic soils (oxisols) of the tropics generally (Sanchez 1976).

The development of strongly weathered soil mantles from most rock types includes several weathering stages (Jackson and Sherman 1953). As secondary minerals form in the weathering zone, there is an initial increase in the availability of plant nutrients, but this gradually decreases as the supply of weatherable minerals is depleted (Stark 1978). Such weathering patterns initially induce progressive changes in vegetation toward higher-fertility-demanding vegetation communities that eventually reach a climatically controlled maximum of vegetative biomass. As depth of weathering increases, the soil is no longer able to meet the nutrient demands of the climax vegetation and, as a consequence, the trend in succession is away from the biomass maximum.

In fertile soils (i.e., soils still containing both high levels of available plant nutrients and weatherable minerals that can replace nutrients immobilized or lost by leaching), plant succession progresses toward a biomass maximum that is determined by climate and rate of nutrient supply. While disturbance in the progressive phases will retard advancement to a biomass maximum, it is unlikely to divert it unless the disturbance also leads to marked changes in rates of nutrient and water supply. Examples of this kind of succession include old fields in the temperate areas (McIntosh 1980) and the recovery following shifting cultivation in rain forests on fertile soils.

However, when the vegetation has reached the biomass maximum, the weatherable

TABLE 1

BIOLOGICAL RESPONSES TO SOIL AGING IN THE DUNE SYSTEMS AT COOLOOLA, QUEENSLAND

DUNE RELATIVE AGE	MORPHOLOGY OF DUNES	VEGETATION STRUCTURE	RELATIVE BIOMASS (maximum = 100)	VEGETATION UPPER STRATUM HEIGHT (m)	SUCCESSION TYPE*
1	Mobile or recently vegetated dunes	Closed, shrubby woodland	20	9	P
2	Weakly eroded vegetated dunes	Grassy, open forest	30	15	P
3	Slightly eroded vegetated dunes	Grassy, open forest	60	28	P
4	Moderately to strongly eroded vegetated dunes	Very tall, open forest	100	35	P
5	Remnants of severely eroded dunes	Shrubby woodland	40	20	R
6	Whale back sand hills; remnants of very severely eroded dunes	Low, shrubby woodland or heath	10	8	R

*P = progressive; R = retrogressive.

minerals and their derivatives in the root zone become depleted by leaching, and the system becomes increasingly dependent on atmospheric accessions, on strategies that reuse nutrients already in the organic cycle, and on nutrients slowly mobilized from sesquioxides (Bowen 1980, Stark and Jordon 1978). With time, the system may appear to become more stable but is increasingly vulnerable to disturbance. Accelerated retrogressive succession must occur following disturbance unless the disturbance also introduces new sources of nutrients back into the root zone. Gross disturbance associated with land clearing on deeply weathered soils rapidly accelerates retrogressive trends and in many instances brings catastrophic change; for example, the failure of many rain forest areas on lateritic soils to regenerate following clearing and burning (Gillison 1975, Uehara and Gillman 1981).

COOLOOLA SOILS AND VEGETATION

The podzol chronosequence on coastal sand dunes in southern Queensland (Thompson 1981) provides an opportunity for demonstrating progressive as well as retrogressive successional change. Colonizing plants on the bare sands of mobile dunes are replaced by several stages of floristically and structurally distinct woodlands and grassy forests to reach very tall *Eucalyptus pilularis* forests that represent the climatic biomass maximum on freely drained sites (Walker et al. 1981; see also Table 1).

Weathering of the vegetated dunes leads to the development of podzols (Thompson 1983). These soils have A_1 horizons of clean quartz sand mixed with decomposing debris; bleached A_2 horizons of clean quartz sand; B_2hir horizons of accumulated organic, iron, and aluminum compounds; and C horizons of yellowish-brown, sesquioxide-coated sands (Brewer and Thompson 1980, Thompson and Hubble 1980). As weathering proceeds, depth to B horizon increases and there is a large increase in thickness of bleached A_2 horizon relative to that of the A_1 and B_2hir horizons (Figure 2). In these soils, plant nutrients can be held only in the organic compounds of A_1 and B_2hir horizons and on the sesquioxides of the B_2hir and C horizons. At the vegetation phase of biomass maximum, soil weathering has led to the development of A_1 and A_2

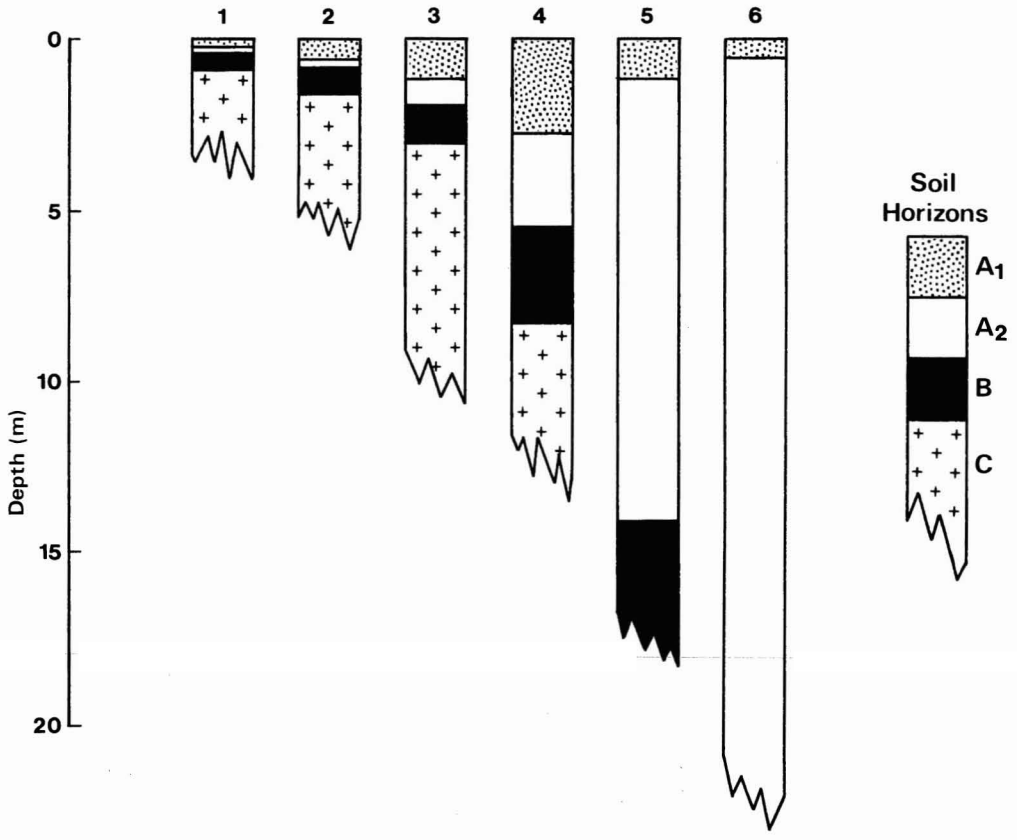

FIGURE 2. Soil development age sequence on ridge crests in the dune systems at Cooloola, Queensland (after Walker et al. 1981).

horizons with combined thicknesses in excess of 5 m, i.e., the depth to the B horizon is >5 m. Because of (*a*) the slow rate of nutrient release from the decomposition and mineralization of annual litter fall and (*b*) the thick A_2 horizons limiting root access to slowly available nutrients in the B_2hir and C horizons, the root zone is no longer able to meet the nutrient demands of the *Eucalyptus pilularis* forest let alone sustain a greater biomass. The rate of leaching losses then exceeds the rate of supply from further weathering and atmospheric accession, and the system becomes fragile and vulnerable to change that can be only retrogressive (Walker et al. 1981). The older (Pleistocene) sand dune systems at Cooloola show this clearly in the development of "giant" podzols and increasingly depauperate vegetation accompanying the continued soil weathering and increasing depth to B horizon (Table 1, Figure 2).

Particular assemblages of vegetation have been found to be associated with each of the dune systems in the age sequence (Walker et al. 1981), and there is a similar relationship between soil invertebrate fauna and dune age (P. J. M. Greenslade and Thompson 1981, P. Greenslade and Thompson 1981). In applying the Cooloola example to other landscapes with different limiting factors and recovery mechanisms, a clear distinction needs to be made between (*a*) progressive developmental stages with potentially available weatherable minerals and (*b*) retrogressive stages where the nutrients are largely in the organic cycle and where nutrient losses outweigh gains. The hypothesis is that when

ecosystems in the progressive stage are disturbed, multiple pathways of vegetation succession can exist but will eventually converge toward the biomass maximum. Disturbance in the retrogressive state results in pathways that diverge away from the maximum biomass.

The present-day communities at Cooloola have resulted from processes operating over millennia. However, in retrogressive systems, human disturbances may compress the time intervals of community change to decades. We attempt to draw an analogy between the aging sequences evident at Cooloola and New England dieback prevalent in the tablelands of New South Wales, by suggesting that in many areas dieback may have been accelerated by human-induced environmental changes on retrogressive ecosystems.

THE NEW ENGLAND AREA

Soils

A diversity of rock types has been exposed to weathering and soil formation in the New England area. These include a range of metamorphic and sedimentary rocks (such as greywackes, slates, and mudstones), acid intrusives (such as granites, granodiorites, and porphyries), and basic lavas (such as basalts and trachytes) (Jessup 1965).

The mineralogy of each of these rock types sets a potential ceiling to the contents of clay minerals and most plant nutrients that can be released by weathering to the developing soil. Whether these potential contents are reached or remain in the soil systems depends on weathering trends and erosion rates, largely governed by the other factors of soil formation (Jenny 1980). In the New England area, variations in the effects of climate on soils are mainly associated with the decline in rainfall from east to west and with a gradient in temperature from lower to higher elevations. Soils are more leached under the higher rainfall, and the content of organic matter of the surface horizons is greater at elevated sites.

Most of the present topography has developed since the lava flows of the Tertiary, as the streams cut through the variety of rocks to their present positions. Erosion of the landscape has led to areas of the same rock type being exposed to soil formation for different periods and to differences in rates of leaching, drainage, erosion, and sedimentation between hill crests, slopes, and valley floors.

As a consequence of the variability in soil forming factors in the New England area, a great diversity of soils occurs (Gibbons and Hallsworth 1952, Jessup 1965, McArthur 1964, McGarity 1977), with a range in morphological, physical, and chemical features that encompasses more than 20 of the Australian great soil groups (Stace et al. 1968).

Most of the soils developed on sedimentary, metamorphic, and acidic intrusive rocks and on trachyte lavas are low in a number of the nutrients essential for plant growth, especially phosphorus (Jessup 1965, MacArthur 1964). In most of these soils, much of the limited nutrient reserve that had been pumped up from the root zone was in the organic cycle when agricultural and pastoral development began. The soils had a variable, but generally small, nutrient reserve associated with the organic matter of the A_1 horizon, but the subsoils in the root zone were largely depleted of readily available nutrients and weatherable minerals. The nutrient levels of the older soils on basalt were similarly low; lateritic weathering had led to the loss of bases and the immobilization of phosphorus and elements (such as molybdenum) in the sesquioxide fraction. Only the younger soils on basalt and on some sedimentary rocks and alluvium, particularly in the drier zones, had moderate to high levels of available plant nutrients. The soils of the remainder of the region are believed to have been poised for rapid nutrient rundown when the native ecosystems were disturbed.

As pastoral use progressed, a decline in soil fertility has occurred (Parbery 1939), which has led to changes in land use in some areas (McArthur 1964).

Spencer and Barrow (1963) showed deficiencies of phosphorus and sulfur throughout the podzolic and solodic soils, whether derived from a range of indurated sedimentary rocks or from various granites and por-

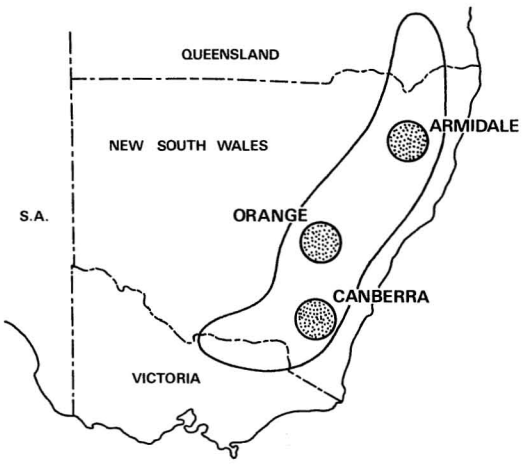

FIGURE 3. The main areas of New England dieback, with the tableland areas around Canberra, Orange, and Armidale indicated.

phyries. Deficiencies were less pronounced in solodic soils on adamellite porphyry and on soils derived from basalt. Responses to boron, potassium, and molybdenum occurred at some sites (2 out of 19). These studies indicate the progressive exploitation of the nutrient reserves in the surface organic matter and the inability of the shallow-rooted introduced and volunteer pasture species to secure nutrients from the depleted subsoils.

Vegetation

When pastoral and agricultural settlement began, most of the area carried grassy woodlands, open forests, and forests in which various species of eucalypts were the dominant trees (Baur 1962, Williams 1963), but there was a great diversity of vegetation types from open, grassy woodlands and heaths through to wet sclerophyll forests and rain forests. The vegetation communities appear to have been closely related to the soil pattern, reflecting differences in soil water and nutrient supply as well as the east–west rainfall gradient and temperature variations with altitude.

We suggest that prior to European settlement, plant succession had reached or passed the stage of maximum biomass development on all the old deeply weathered soils and on the moderately deep soils developed on all the parent materials except some basalt and young alluvium. Consequently, most of the vegetation was in various stages of retrogressive decline in terms of standing biomass or was about to retrogress. Progressive stages of succession were probably associated with most of the shallow soils, the moderately deep soils on basalt, and those on alluvium. The relative areas of adjacent communities in retrogressive or progressive stages of succession would be expected to vary according to soil nutrient status and weathering stage from one rock type to the next and from wetter to drier areas.

New England Dieback

New England, or rural, dieback is primarily a decrease in the leafiness of eucalypts in tableland areas predominantly used for grazing or agriculture; it is particularly common in the tablelands of eastern New South Wales above 800 m (Clark et al. 1981) (Figure 3). Crown decline generally commences at the outer tips of branches and progresses down the tree crown. It may or may not eventually lead to death of the trees. There is apparently no single cause of dieback, and two or more factors may interact to produce the recognizable symptoms (Anon. 1979). Boyd (1965) has made the important point that, while dieback has reached dramatic proportions over the past 20 yr, it has been present in the New England area for a long time. Reports by Norton (1886) and Macpherson (1885) indicate that even 100 yr ago, concern was being expressed about the future of Australian forests because of the occurrence of dieback.

Crown dieback of eucalypts on the New England tablelands is well documented (Anon. 1979, Boyd 1965). The susceptibility of various eucalypt species to dieback has been reported (Williams and Nadolny 1981), and possible links with land use and physical site factors have been investigated (Clark et al. 1981, Duggin 1981, Mackay 1978). Duggin (1981) examined the relationship between dieback incidence and land use intensity (degree of clearing of trees, fertilizer applica-

tion, domestic animals per hectare, etc.), and showed that dieback was related to the intensity of land use. He interpreted these results as evidence that land use had induced "environmental shifts," and that under the changed environmental conditions dieback and tree death occur more readily. Dieback is known to affect a range of tree ages, and trials to test the survival of juvenile eucalypts have been described by Roberts and Sawtell (1981).

New England dieback is often attributed to massive and repeated defoliation by leaf-grazing insects, particularly leaf beetles (chrysomelids) and christmas beetles (scarabs) (Clark et al. 1981). A general link between dieback symptoms and insect grazing has been described (Carter, Edwards, and Humphreys 1981) as follows: In spring, new leaf growth is eaten by larvae and adult stages of leaf-eating chrysomelid beetles and other insects. In early summer, mature leaves and regrowth leaves are eaten by mature scarab beetles as part of a cycle in which their larvae feed on grass or pasture species roots. In middle to late summer, the trees affected by previous insect attacks produce a flush of juvenile leaves and these are eaten by a new generation of chrysomelid beetles. Later flushes of leaves may be killed by frosts, which are common in late autumn and through winter. Repetition of this predation cycle together with other stresses may lead to tree death. The rapid spread of improved pastures in the New England area made possible by the application of superphosphate and the introduction of leguminous pasture species has led to an increased food source for scarab and other beetles which utilize herbage roots in part of their life cycle. This increased population of beetles and the progressive removal of trees for pasture establishment places additional pressure on the remaining trees. The insect populations are such that control by birds is not possible in most situations (Ford 1981). Interactions between eucalypt leaves, grass, beetle, and bird biomass, and possible systems outcomes have been modeled by Trenbath and Smith (1981).

Richards (1981) defined New England dieback in functional terms as an ecological condition in which a significant proportion of the primary production of the tree stratum is diverted through the insect-grazing food chain, instead of passing directly through the decomposition subsystem. The change in pathways and the reduced capability of trees to capture and store energy are seen as major factors causing tree decline. The trigger mechanism responsible for this diversion of photosynthate from normal pathways of energy flow is, in Richards' opinion, the key to understanding the dieback phenomenon. Leaf grazing by insects is therefore viewed as a symptom of breakdown in the normal regulatory or recovery processes of ecosystem function, rather than the prime cause of the phenomenon.

APPLICATION OF THE COOLOOLA MODEL TO NEW ENGLAND DIEBACK

The Cooloola vegetation/soil relationships provide an overall model for plant succession in old landscapes. The canopy dieback phenomenon can be placed in such a model relative to various interacting causal agents and processes. Ample evidence exists to show that many of the soils in the New England tablelands are highly weathered, and by analogy with Cooloola we suggest that much of the vegetation is in a retrogressive successional phase. The forests and woodlands under these conditions are highly dependent upon the maintenance of natural processes for the retention and recycling of nutrients, most of which are associated with organic matter in the A_1 horizon. The extension of agriculture into these areas is likely to have brought major changes to both the soils and soil processes and their equilibrium states. Tree clearing, the introduction of domestic livestock and pasture species, the alteration of natural fire patterns, and the application of large quantities of phosphate fertilizer to benefit shallow-rooted species, are likely to have grossly altered the soil water balance (Burch and Nicholls 1981), the population dynamics of defoliating insects (Carter, Edwards, and Humphreys 1981), the relative competitiveness of grass and tree seedlings

(Walter 1971), and many aspects of the soil biota (Griffin 1972). The high levels of fertilizer application have almost certainly retarded the activity of naturally occurring microorganisms, especially mychorrizas, which are critical to the plant uptake and cycling of nutrients in native forests (Jehne 1981). The fertilizers may also accelerate the decomposition of nutrients held in the organic matter, as well as decreasing the root: shoot ratios of eucalypts and increasing the attractiveness of the foliage to leaf-eating insects. Consequently, the various canopy dieback symptoms and agents observed in the New England tablelands represent the mechanisms by which changes are occurring in retrogressive ecosystems that have been severely disturbed. The observations of dieback occurring at a reduced level in intact forests today (Duggin 1981), the occurrence of dieback over 100 yr ago in the area (Boyd 1965), and its general absence in areas away from the tablelands (Clark et al. 1981), add support to the retrogressive succession hypothesis. We would expect to find a range or mosaic of retrogressive (degrading) communities associated with soils at different weathering stages on each of the parent materials. Thus, the incidence and severity of dieback should be variable but should form a pattern that generally conforms with the distribution of soil types but is not necessarily apparent at soil group level. Differences in climatic and edaphic factors (rainfall, slopes, drainage lines, hot/cool aspects, etc.) should overprint this mosaic, and interactions due to kinds and levels of disturbance further alter the rates of system decline. In general, we would expect to find differences in species responses to dieback that fit into the ecological provinces in the area as described by Duggin (1981).

If this hypothesis is correct, then application of the modeling approaches of Trenbath and Smith (1981) and Landsberg and Wylie (1983) and the theoretical framework of Richards (1981) to explain the causality of New England dieback requires additional parameters to take into account the declining soil resource and the changes in soil processes against which all other factors interact.

The inference is that the system decline is not a phasic phenomenon, such as that described for regrowth dieback in Tasmanian forests (Jehne 1976). Also, the decline is probably not readily reversible given a continuation of the present-day grazing industry in the New England area. Current areas of forest can be kept in their present slow rate of decline only by minimal disturbance. Reducing the rate of the decline in cleared areas is possible only by changing grazing management techniques to utilize weak points in the life cycle of the leaf-eating insects (Roberts 1979) or by introducing exotic (especially deciduous) trees or native trees from old weathered landscapes that have leaves unattractive to insects.

We postulate that a similar relationship to that which exists between canopy dieback vegetational successional phase and soil weathering stage in the New England tablelands of New South Wales also occurs in the tablelands around Orange and Canberra (Figure 3). The relationship between canopy dieback incidence and soil "biological age" could be statistically investigated by selecting a range of sites that reflect landscape differences (geology, slope, aspect, drainage pattern, etc.) and testing the level of correlation between soil attributes selected to reflect soil weathering stage (not generalized soil groups) and degree of canopy dieback (defoliation level and tree death). The soil attributes should be selected as those likely to be important to tree physiology (water balance especially in lower soil layers, gross and micronutrient levels and turnover rates in various soil layers, mychorrizal activity, pH, etc.) and to reflect soil weathering stage (mineralogy, weatherable mineral content, phosphorus compounds, etc.).

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